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Predation by Harbour Seals and Sea Lions on Adult Salmon in Comox Harbour and Cowichan Bay, British Columbia

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PREDATION BY HARBOUR SEALS AND SEA LIONS ON ADULT SALMON IN COMOX HARBOUR AND COWICHAN BAY, BRITISH COLUMBIA

by

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ABSTRACT

Bigg, M. A., G. M. Ellis, P. Cottrell, and L. Milette. 1990. Predation by harbour seals and sea lions on adult salmon in Comox Harbour and Cowichan Bay, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1769: 31 p.

The movements, feeding behaviour and predation rate on prespawning salmon by harbour seals (*Phoca vitulina*) at Comox Harbour and Cowichan Bay and by sea lions (*Zalophus californianus*, *Eumetopias jubatus*) at Cowichan Bay were examined during 1989-90. Tidal variation largely governs the daily movement of harbour seals over the estuaries. Sea lions tended to remain in slightly deeper water than harbour seals and their movements were affected less by tides. Peak harbour seal abundances of 750 and 175 were recorded in Comox Harbour and Cowichan Bay respectively. A maximum of 30 sea lions were counted at Cowichan Bay. The seasonal movement of these pinnipeds into the estuaries coincided with the migration of prespawning salmon into nearby rivers. Harbour seals and sea lions fed on salmon mainly along the outer edge of the estuaries, although harbour seals also commonly fed in the lower reaches of the Puntledge River which drains into Comox Harbour. Two to four harbour seals usually preyed together upon a single salmon. A combination of cooperation and opportunism seems involved in group predation. Sea lions tended to feed individually. Based on the number of salmon seen eaten hr^{-1} in 1989, an estimated 46% of the fall run of chinook, 4% of pinks, 8% coho and 7% chum salmon were taken by harbour seals at Comox Harbour. In Cowichan Bay an estimated 1% of coho and 1% of chum were eaten by harbour seals and 3% of coho and 3% of chum were eaten by sea lions during 1989. The fall run of chinook salmon at Comox Harbour were particularly vulnerable to predation by harbour seals due the low number of fish and their availability for predation in both the Comox Harbour estuary and the slow moving Puntledge River.

RÉSUMÉ

Bigg, M. A., G. M. Ellis, P. Cottrell, and L. Milette. 1990. Predation by harbour seals and sea lions on adult salmon in Comox Harbour and Cowichan Bay, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1769: 31 p.

Les déplacements, le comportement alimentaire et le taux de prédation des saumons avant la fraye par des phoques communs (*Phoca vitulina*) dans le havre Comox et la baie Cowichan, et par des otaries (*Zalophus californianus Eumetopias jubatus*) dans la baie Cowichan ont été étudiés au cours de l'année 1989-1990. La variation tidale régit en grande partie le déplacement quotidien des phoques communs dans les estuaires. Les otaries avaient tendance à demeurer dans des eaux un peu plus profondes que les phoques communs et leurs déplacement étaient moins touchés par les marées. Une abondance maximale de respectivement 750 et 175 phoques communs a été enregistrée dans le havre Comox et dans la baie Cowichan. On a dénombré un maximum de 30 otaries dans la baie Cowichan. Le déplacement saisonnier de ces pinnipèdes dans les estuaires a coïncidé dans la migration des saumons avant la période de fraye dans les cours d'eau avoisinants. Les phoques communs et les otaries se nourrissaient surtout sur le bord extérieur des estuaires, même si en général les phoques communs se nourrissaient aussi dans les tronçons inférieurs de la rivière Puntledge qui se jette dans le havre Comox. En général, un seul saumon est la proie de deux à quatre phoques communs. Dans la prédation de groupe, il semble qu'il y ait à la fois un mélange de collaboration et d'opportunisme. Les otaries avaient tendance à rechercher leur nourriture séparément. D'après le nombre de saumons consommés par heure, en 1989, on a estimé que 46% de la remonte d'automne des saumons quinnats, 4% des saumons roses, 8% des saumons cohos et 7% des saumons kétas ont été prélevés par des phoques communs dans le havre Comox. Dans la baie Cowichan, on a estimé à 1% le nombre de saumons cohos et de saumons quinnats ingérés par des phoques communs, et à 3% les saumons cohos et kétas ingérés par des otaries en 1989. La remonte d'automne du saumon quinnat dans le havre Comox était particulièrement vulnérable à la prédation par les phoques communs en raison du faible nombre de poissons et de leur disponibilité à la prédation dans l'estuarie du havre Comox et dans la rivière Puntledge à débit lent.

INTRODUCTION

Harbour seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*) are known to feed on salmon in estuaries and rivers during summer and fall before they spawn (Imler and Sarber 1947; Fisher 1952; Spalding, 1964; Jameson and Kenyon 1977; Gearin *et al.* 1988). This predation has resulted in numerous population control programs in the past, (Bonnot 1928; Imler and Sarber 1947; Bigg 1969; Bigg 1985). However, little is known about how these pinnipeds hunt salmon or of the impact of their predation on salmon stocks in such areas.

During 1989, we examined the hunting behaviour and impact of predation on prespawning salmon by harbour seals at Comox Harbour and Cowichan Bay and by California and Steller sea lions at Cowichan Bay, British Columbia. In Comox Harbour, predation was examined on chinook (*Oncorhynchus tshawytscha*), pink (*O. gorbuscha*), coho (*O. kisutch*) and chum salmon (*O. keta*) and in Cowichan Bay on coho and chum salmon.

The field studies involved: 1) censuses of harbour seals and sea lions to determine the seasonal variation in abundance relative to salmon migrations; 2) observations of pinniped predatory activities; and 3) kill rates on salmon to assess predation impact. The value of using direct field observations to describe pinniped predation is discussed.

METHODS

Field observations were made usually by 2 people (range 1-4) from small (5 m) power boats or from vantage points on land. Visual censuses were undertaken between 5 January 1989 and 23 February 1990 at Comox Harbour and between 2 August 1989 and 18 January 1990 at Cowichan Bay. Behaviourial observations were undertaken during daylight hours between 11 August and 28 December 1989 at Comox Harbour and 28 September and 2 January 1990 at Cowichan Bay. Observations from boats were made by eye and with the aid of binoculars and observations from land with a 15X spotting scope mounted on a tripod.

The behaviourial data recorded included the manner by which salmon were pursued, captured and eaten, the time and location of each kill, the number of individual pinnipeds involved in each kill, the species of salmon consumed and the observational effort to the nearest 0.1 hr. All species identifications of salmon were made from boats. Species were identified using: 1) visual identification of the distinctive scale patterns, coloration and size of each species (see Hart 1973); 2) retrieved carcasses; and 3) scales recovered using a fine mesh dip net at the kill sites.

Table 1 presents the results of an accuracy test for the identification of salmon species by field observers and a scale reader. The scale reader identified all 18 scale samples to the correct species without

knowledge of the species identification based on carcass recovery. Based on subsequent scale identification, field observers correctly identified visually 24 (92%) of the 26 kills for which no carcass was retrieved. Thus, the scale reader and field observers were likely to have made few errors in salmon species identification. Salmon kills which could not be identified to species were recorded as unknown salmon species kills.

Table 1. Test for the accuracy of salmon species identification for harbour seal and sea lion kills in Comox Harbour and Cowichan Bay during 1989.

Salmon species	Identification basis		Identification basis	
	Carcass	Scale	Scale	Visual
Chinook	13	13	8	8
Pink	1	1	10	11
Coho	2	2	7	5[1]
Chum	2	2	1	2
Total	18	18	26	26

[1]Two coho salmon were incorrectly identified, one as a chum and the other as a pink salmon.

We examined the relationship between the number of seals feeding together (group size) and the species of salmon eaten in the comox Harbour. First we used a 2-way ANOVA to test whether there was a difference between group size in the Comox estuary and the Puntledge River. Next we calculated a Spearman's rank correlation to test whether there was a relationship between prey size (ranked from 1 to 4, smallest to largest) and group size. Finally a 2-way ANOVA was used to test whether harbour seal group sizes differed in the Comox Harbour compared to Cowichan Bay.

When estimating predation impact, we apportioned the unknown salmon species to the known species composition by assuming that the species composition of the unknown salmon kills was the same as for the known salmon species kills. Apportioning was stratified by 0.5 month intervals and by estuary and river. For example, the number of individuals of unknown species recorded in the Comox Harbour estuary during 1-15 September were apportioned to the number killed for the known salmon species recorded during that time and place based on the known species composition of the kills at that time and place.

To estimate predation impact during daylight hours, we used the number of daylight hours between civil twilight times. Civil twilight occurs shortly after sunset and shortly before sunrise. The civil twilight times for Nanaimo were provided by the Canadian Department of Transport, Cassidy Airport, British Columbia. We also used tide height to estimate predation impact in the Puntledge River. The tide heights used were those for Little River about 8 km to the north and estimated by the Department of Fisheries and Oceans, Institute of Ocean Sciences, Sidney, British Columbia.

Predation impact was determined from the estimated total number of individuals of each salmon species eaten relative to the total number of individuals of each species available for consumption. The total number

available for consumption was the sum of the number of individuals estimated to have been consumed and the number of individuals known to have escaped for spawning as recorded by fisheries managers.

RESULTS

1. Study sites

We used two study sites at Comox Harbour, the estuary and the lower reaches of the Puntledge River and one site at Cowichan Bay, the estuary. The estuary at Comox Harbour is about the same width at its outer edge as the estuary at Cowichan Bay, although the total estuary area at Comox Harbour is slightly larger than at Cowichan Bay (Fig. 1A-B). At both estuaries, the substrate consists of a mosaic of mud, sand and small rocks. The inland borders consist of shallow sloping beaches with grassy hummocks and the outer boundaries (10 m depth) drop into deep water. At low tides much of the estuaries are exposed. At this time the rivers cross the estuaries in meandering drainage channels. At high tides, the estuaries are completely flooded. Small commercial fishing vessels, tugs and barges travel across the Comox Harbour estuary and into the lower reaches of the Puntledge River during high tide. However, shallow water prevents commercial vessel traffic from moving into the lower reaches of the Cowichan River or Koksilah River which drain into Cowichan Bay.

2. Daily use of sites by pinnipeds

The daily movements of harbour seals at Comox Harbour and Cowichan Bay were governed largely by the rise and fall of tides. At the lowest tides, when much of the two estuaries were exposed, harbour seals gathered in the shallow waters along the outer edge. The main activities in these shallow waters appeared to be resting, slow swimming and feeding. As the tide rose and flooded over the estuaries, seals moved inshore although some still remained in the outer third. Some seals entered the Puntledge River as the tide rose, but few if any appeared to enter the Cowichan River and Koksilah River.

Harbour seals foraged for salmon mainly along the outer edge of the estuary at Comox Harbour and in the lower reaches of the Puntledge River (Fig. 1A-B). In Cowichan Bay, they also fed mainly along the outer boundary of the estuary, with a few foraging near the entrances to the Cowichan and Koksilah Rivers. Occasionally many of the seals in both estuaries rested in the shallow waters (<2 m depth) near the inland boundaries. Seals did not haul out on the substrates at Comox Harbour or Cowichan Bay, but frequently hauled out on logbooms moored in both estuaries.

Tidal variations in the estuary at Cowichan Bay appeared to have less effect on the daily movements of sea lions than on harbour seals. Like seals, sea lions remained swimming at the outer edge of the estuary, but

tended to prefer slightly deeper waters. Sea lion activities consisted mainly of resting in floating rafts, grooming and foraging. The main salmon foraging area used by sea lions in Cowichan Bay overlapped most of that used by the harbour seals. Sea lions did not haul out on the estuarine substrate or logbooms.

3. Seasonal use of sites

During 1989, the number of harbour seals at Comox Harbour remained relatively constant between December and July, increased in August and again in October to a maximum of 750 seals, then decreased precipitously in November (Fig. 2). Fewer data exist for Cowichan Bay, although the pattern of change in numbers of harbour seals during 1989-90 seems similar (Fig. 3). The maximum number reached at Cowichan Bay was 175 seals.

Sea lions moved into Cowichan Bay during the first half of October, reached a peak of 30 individuals in late October, declined in November-December and were gone by January. This population consisted mainly of California sea lions plus a few Steller sea lions. California sea lions comprised 67% and 91% of the total number of sea lions present in two censuses.

A comparison between the seasonal changes in number of harbour seals and timing of salmon spawning in the upper rivers (Figs 2-3) suggests that seals moved into Comox Harbour and Cowichan Bay to feed on migrating salmon. It should be noted that spawning time in the upper reaches of the rivers lags (perhaps 1-2 weeks) the migration timing of each salmon species through the estuaries. At Comox Harbour, seal numbers increased in August at about the same time the main pink salmon biomass occurred. The sharp peak in seal numbers in October corresponds with the main migration time of coho and chum salmon. The decline in seal numbers in November corresponds with the passage of all salmon species through the Comox Harbour estuary and the lower reaches of Puntledge River. At Cowichan Bay, harbour seal numbers increased mainly during October when the peak biomass of coho and chum salmon passed through the estuary. Seal numbers declined in December following the passage of most salmon through the estuary.

A small increase in the number of harbour seals during July-August in Comox Harbour and Cowichan Bay was probably due to the addition of pups born at this time. The increase is likely in the order of 25% of the prepupping population size (Olesiuk *et al*. 1990a). We have no evidence that seals move into these areas to pup.

4. Effort and kills

A total of 165 hours of observation were made and 342 kills noted in Comox Harbour and Cowichan Bay (Table 2). Observations took place between 5 am and 7 pm, although 72% of the effort was made between 10 am and 1 pm. The

schedule for collecting data on predation rate consisted of frequent short periods of observation. A total of 35 days were spent observing in the estuary at Comox Harbour with a mean observation period of 1.9 hr per day (max 6.7 hr), 24 days at the Puntledge River with a mean of 1.4 hr per day (2.5 hr) and 21 days at Cowichan Bay with a mean of 3.1 hr per day (6.5 hr).

5. Species eaten

We observed harbour seals eating chinook, pink, coho and chum salmon in Comox Harbour and chinook, coho and chum salmon in Cowichan Bay. Pink salmon do not spawn in the rivers draining into Cowichan Bay. Sea lions were seen to eat coho and chum salmon. Although a few sockeye (*O. nerka*) enter Comox Harbour and small numbers of steelhead trout (*Salmo gairdneri*) enter Comox Harbour and Cowichan Bay in summer and fall, we did not observe any predation by harbour seals or sea lions on these species.

Chinook and coho salmon are comprised of jacks and non-jacks. Jacks are small (see Table 4) precocious males (ages in years: coho = 1.0 or 0.1; chinook = 0.1 or 1.1). We did not observe any predation on jack chinook or jack coho. Thus, our analyses on predation rate refer to non-jacks only.

6. Foraging behaviour

Foraging behaviour by harbour seals and sea lions was divided into: search, pursuit, capture and consumption. Search behaviour was characterized by a steady swimming speed, brief periods at the surface and remaining within a small area. Pursuit consisted of rapid bursts of swimming speed with sudden turns and a fleeing salmon frequently visible in front of the pinniped. Captures were evident when the pinniped surfaced with a salmon in its mouth. Often gulls flocked over the kill site waiting to feed on scraps of salmon. Consumption was characterized by frequent splashing by the pinniped at the surface with fragments of salmon visible in the pinnipeds' mouth. We saw feeding on salmon throughout our observation times for harbour seals and sea lions which were between 5 am and 6 pm and 9 am and 3 pm respectively.

A. Harbour seals

Harbour seals foraged in groups during 80% of the 158 salmon kills recorded in Comox Harbour and Cowichan Bay (Table 3). Group size was defined as the maximum number of seals present during a foraging bout which involved a kill. The typical group size of harbour seals was 2-3 individuals, but groups of up to 6 were common.

Probability plots showed that the underlying distribution of group sizes was not normal. Since the data were small counts, a square root transformation ($X=\sqrt{X+0.5}$) was used to achieve normality where X is group size.

The 2-way ANOVA on the transformed data showed no difference between group sizes observed in the Puntledge River and group size in the Comox estuary ($F_{1,106}$=0.74, P=0.39) and there was no interaction between the areas hunted and prey species caught ($F_{3,106}$=0.117, P=0.43). However, the number of harbour seals observed together did differ depending upon the species of salmon caught ($F_{3,106}$=11.32, P<0.001). In particular, group sizes associated with pink salmon were significantly smaller than for any other species of salmon (Post-hoc comparison: $F_{1,106}$=29.72, P<0.001). But the difference between group sizes when hunting chinook, coho and chum were not deemed significant ($F_{2,86}$=1.51 P=0.23).

Figure 4 shows the mean group size of harbour seals feeding on pink, coho, chum chinook salmon in the Comox waterway. Data from the river and estuary were pooled to increase sample size. This is justifiable based on the similarity of residual plots for the areas as well as the results of the 2-way ANOVA.

The number of harbour seals observed foraging together in the Comox Harbour appears to depend upon the size of the salmon captured. The larger the salmon, the more seals present. This is seen in Figure 4 where prey species are arranged in size from smallest (pink) to largest (chinook).

A Spearman's rank correlation between prey size and foraging group size was calculated by ranking the prey species from 1 to 4 (smallest to largest). This was done because the exact size of the salmon captured was not known. The results further support the observation that group size was indeed dependent upon the size of the salmon captured ($r_{s,114}$=0.415, P<0.001).

We tested by 2-way ANOVA whether the area fished (Cowichan Bay and the pooled Comox region) and the species caught (chum, coho and chinook) affected the foraging size. The results show no difference between area, species caught or the interaction of area and species. Note that the sample size in Cowichan Bay is small (n=21) and that the test has very little power. However, we have no reason to believe that feeding behaviour is any different here than in the Comox, although salmon species composition may differ.

Searching and pursuit by harbour seals were undertaken largely out of view and thus were not often recorded. Searching tended to be solitary, although groups of up to 4 seals were seen. Searching was undertaken by relatively few individuals at any one time. In Comox Harbour a maximum of about 20 seals were seen searching even though a hundred or more individuals might be swimming or resting nearby. Similarly, a maximum of only about 10 were seen searching in Cowichan Bay. We were unable to estimate the duration of searches. Pursuit usually involved more than one individual and the group size often increased as the pursuit progressed. Seals followed the fleeing salmon and shifted their direction in unison as the salmon changed directions. Salmon were frequently driven into shallow water (<1 m) where they could be more easily captured. Pursuit rarely lasted more than 1 min.

In a group capture, the salmon was brought to the surface by a single seal while the other seals remained nearby and rarely attempted to steal the fish. The most common method of capture, as indicated by direct

observation and recovery of carcasses, was to grab the salmon by its underside, typically by the throat or belly. The largest salmon carcass recovered during a kill was a chinook weighing 12.7 kg preyed upon by five seals.

Consumption began when the seal with the salmon began tearing out its throat or belly. The seal did this by grasping the fish in its mouth, using its front flippers to tear the flesh apart and by breaking the fish apart with head shaking motions. At this point, other seals joined the feeding. Group sizes tended to be largest during consumption.

Group foraging in harbour seals appears to involve a combination of individual cooperation and opportunism. Cooperation was suggested by the general coordination and lack of apparent aggression between individuals within groups during feeding. Opportunism was suggested by the tendency for an increasing number of individuals to join a group as foraging progressed. In one instance, opportunistic feeding was prevented when a seal swam to join another which was feeding on a salmon, but was then chased away. We do not know whether the foraging groups remain together during nonforaging times. When not foraging the seals appear to be solitary, although loose groupings could still exist and not be obvious. The natural markings of swimming individuals are rarely distinctive enough to determine which individuals associate.

B. Sea lions

Sea lions in Cowichan Bay foraged singly during 92% of the 48 salmon kills observed (Table 3). The largest group was comprised of 3 individuals. We were unable to make enough observations to describe typical sea lion searching and pursuing behaviour on salmon. During capture, each sea lion appeared to bring its salmon to the surface, usually held by the head or belly. Within about 15 sec the sea lion made a few sharp snaps with its head, which tore the salmon apart, and then proceeded to consume the salmon. On two occasions individual California sea lions appeared to steal a salmon which had been captured by harbour seals feeding nearby.

7. Impact on salmon

The sequence of analysis to determine the impact of harbour seals and sea lion predation on salmon was: 1) apportion the salmon kills for which the species were unknown to the kills for which salmon species were known; 2) calculate the number of each salmon species killed hr^{-1} by date; and 3) calculate the total number of each salmon species eaten and compare this number to the number of each salmon species available for predation.

A. Apportioning salmon species

Of the 135 salmon kills by harbour seals recorded in Comox Harbour, only 21 required apportioning (see Methods). However, in Cowichan Bay, 94 of 115 harbour seal kills and 61 of the 92 sea lion kills required apportioning. Because of the small number of known salmon species killed,

apportioning values for each salmon species were based on pooled data of seal and sea lion kills in Cowichan Bay during 16 October to 30 November 1989. During this period, 44 of 86 kills were identified to species. The apportioning values for each salmon species were then applied to harbour seals and sea lions for 0.5 month intervals for the period 16 October to 30 November. Such pooling seems valid because both harbour seals and sea lions fed in the same general locality (Fig. 1B) and the main migration timing of the two salmon species fed upon (coho and chum) was similar (Fig. 3). No attempt was made to apportion kills between 16 September and 15 October because too few kills were identified to salmon species.

B. Kill rate by half month intervals

The kill rates by hour of the day were pooled into rates by date for harbour seals in the Comox Harbour estuary and Puntledge River and for harbour seals and sea lions in Cowichan Bay. The rates by date were then pooled into rates by half month intervals (Figs 5-6).

A comparison between the seasonal variation in the kill rate of each salmon species by harbour seals and sea lions for each half month interval (Figs 5-6) and the seasonal passage time of each salmon species through Comox Harbour and Cowichan Bay (Figs 2-3) indicates that the main species fed upon were the most abundant salmon present. For example, chum salmon, which had by far the largest biomass, was eaten at the highest rate.

A decline took place in the kill rate of salmon by harbour seals in Cowichan Bay during the second half of November despite the large biomass of chum salmon present and a continued high predation rate on chum salmon by sea lions. We believe the decline in harbour seal predation rate was biologically meaningful in that it likely resulted from sea lion displacement of some harbour seals from the outer edge of the estuary. Sea lions appeared to steal captured salmon from harbour seals and the vigorous sea lion activity in the main foraging area appeared to discourage harbour seals from feeding there.

Although no estimate was made of the kill rate on each salmon species by harbour seals at Cowichan Bay during late September and early October, chinook was likely to be the main salmon prey. The peak spawning time of chinook was during September (Fig. 3) when 6 of the 8 samples of identified salmon species collected during this time were chinook, one was coho and the other chum. Thus, a few coho and chum were also eaten at this time. No sea lions were present before mid October.

C. Total consumption

The kill rates by half month intervals were used to calculate the minimum and maximum number of each salmon species consumed in Comox Harbour and Cowichan Bay (Table 4). The minimum number of a particular salmon species consumed was taken to be the number of individuals eaten only during daylight hours for those half month intervals in which the species was eaten. The

maximum number consumed was considered to be the number of individuals of the particular salmon species eaten during each 24 hour day for those half month intervals in which the species was eaten.

Estimating the minimum and maximum numbers of salmon eaten by harbour seals in the Puntledge River was a special case because harbour seals could not feed in the river at low tides. Thus, we determined the maximum and minimum numbers of salmon eaten only for those hours during which the tides were high enough for the seals to enter the river and thus to forage on salmon. The tide height which we estimated was sufficient for foraging was about >2.25 m (see Methods for Little River).

Although no kill rates were collected for pink salmon in the Puntledge River during August, kill rates were collected in the Comox Harbour estuary for that time. The rate in the Puntledge River for August was assumed to be 65% of that recorded in the estuary. This percent was the mean (range 45-80%) of the ratio between the rates in the Comox Harbour estuary and the Puntledge River for chinook, coho and chum during September-November when both sites were sampled. The maximum and minimum consumptions of salmon in the estuary at Comox Harbour and the Puntledge River were summed to give an overall figure for Comox Harbour.

The largest number of individuals eaten by harbour seals in Comox Harbour was of chum salmon. Chinook, pink and coho salmon were eaten in smaller numbers, but were of similar magnitudes. In Cowichan Bay, harbour seals ate fewer coho and chum salmon than in Comox Harbour, although chum salmon was still the most commonly eaten. Sea lions in Cowichan Bay consumed mainly chum salmon.

We used the mean of the minimum and maximum numbers of each salmon species eaten as the best approximation for the total number of each salmon species consumed. The mean value was used because, although feeding by harbour seals and sea lions likely took place during the night as well as during day, the feeding rate at night was likely to be lower. Gearin *et al.* (1988) found that while California sea lions fed at night on steelhead trout at the Hiram M. Chittenden Locks, Seattle, the feeding rate was much less than during the day. Some harbour seals were seen feeding at night by workmen at a lumber mill in the lower reaches of the Puntledge River near a well lit logboom during fall 1989. However, because some harbour seals appear to feed cooperatively on salmon, and cooperative feeding presumably requires vision, group foraging may be less effective at night.

Harbour seals appear to eat only a small proportion (<10%) of the available prespawning pink, coho and chum salmon in Comox Harbour (Table 4). Similarly, harbour seals and sea lions are minor predators on coho and chum salmon in Cowichan Bay. However, a large proportion of the fall run chinook were eaten by harbour seals in Comox Harbour.

The actual predation impact by harbour seals on each salmon species may be slightly higher than indicated in Table 4. Not all localities where predation took place could be surveyed at the same time. For example, little effort was undertaken in the upper reaches of the Puntledge River where

some predation is known to take place. Also, about 10% of the area of the estuaries at Comox Harbour and Cowichan Bay could not be observed at any one time and thus a few kills may have been missed. In addition, some coho and chum were probably eaten in Cowichan Bay during September and early October, but could not be estimated because of small sample sizes. Finally, the fall run of chinook in Comox Harbour was assumed to begin in early September (Fig. 2 for fall chinook spawning). However, the end of the summer run and the start of the fall run were not clearly defined and if it actually began in August then the number of fall chinook eaten would be slightly higher.

Still, the total consumption of salmon at Comox Harbour was unlikely to have been substantially biased. Olesiuk *et al.* (1990) used scat analysis to estimate the total biomass of salmon eaten by harbour seals at Comox Harbour in 1988 (see Table 4). In this analysis, the relative importance of salmon and other prey in the monthly diet of harbour seals was determined from the frequency of occurrence of each prey found in the scats. The total biomass of all fish consumed each month was estimated from the energetic requirements for the number of harbour seals present each month. The seasonal variation in the number of seals present in Comox Harbour during 1988, was similar to that seen in 1989. The amount of salmon eaten was determined from the proportion which all salmon comprised of the diet each month. Although salmon can be identified in scats, the identity of each salmon species can rarely be determined. Thus, only an estimate of total salmon consumed could be calculated from scat data. The estimated total biomass consumed based on scat analysis (28.7 mt in 1988; Table 4) revised to account for the 1988 general harbour seal population rate of increase (12.5%; Olesiuk *et al.* 1990a) was 32.3 mt; quite similar to the estimated biomass consumed based on the current study (26.7 mt) in 1989.

However, the total salmon biomass estimated to have been consumed during the current study is probably slightly too low because of biases just mentioned and also because the estimate does not include predation on a small run of summer chinook and perhaps some jack coho and jack chinook. These biases would not be present in the estimate of total salmon consumed based on scat analysis because all salmon species were pooled.

The consumption of individual species of salmon, particularly chinook, using scats, differed quite considerably from that estimated by the current study. It is important to resolve the differences for chinook because it is a prized sport and commercial salmon species. We consider the consumption estimate of each species, based on our study, to be closer to the actual consumption because this consumption was based on direct observation of each species consumed. Estimates based on scat analysis were calculated indirectly from the proportion which each species comprised of the total salmon spawning biomass. That proportion was then applied to the total salmon consumed to provide an estimate of the biomass of each salmon species eaten. Thus, an estimated 0.5 mt of chinook were eaten in 1988, based on scat analysis, but 7.4 mt were eaten in 1989, based on direct field observation.

The main reason that such large differences existed in estimates is that an important assumption which had to be made in scat analysis was unlikely to be true. This assumption was that each species was eaten in the

same proportion as it occurred relative to total spawning biomass. Thus for example, because chinook comprised only a 1.89% of the total biomass eaten in 1988, this salmon species was estimated to have been eaten in very small quantities whereas chum which constituted 82.02% of the total biomass was eaten in large amounts. However, chinook appear to be eaten in a disproportionately large amount compared to chum salmon. This disproportion likely results from the large number of chum salmon swamping the seal predator. It is also possible that chinook were more vulnerable to predation than were chum, the species comprising the largest biomass, because they maybe resident longer in the estuary than chum salmon (see Fig. 2).

Discussion

1. Seasonal movements

Harbour seals, California sea lions and Steller sea lions seasonally appear to move into estuaries and rivers located along their range mainly to feed on seasonal increases in prey abundance in these areas. These pinnipeds are opportunistic feeders on a wide variety of fish and cephalopods (Boulva and McLaren 1979; Olesiuk *et al.* 1990b; Antonelis *et al.* 1984; Pitcher 1981). Harbour seals have been reported to move into bays, estuaries and rivers to feed on prespawning salmon, northern anchovy (*Engraulis mordax*), eulachon (*Thaleichthys pacificus*) and other fish (Fisher 1952; Brown and Mate 1983; Beach *et al.* 1985). Similarly, Steller sea lions and California sea lions have been reported to aggregate in estuaries and rivers to feed on eulachon and steelhead trout (Bigg 1985; Beach *et al.* 1985; Gearin *et al.* 1988). Exceptions exist in that harbour seals sometimes concentrate in estuaries mainly to give birth (Rosenthal 1968; Beach *et al.* 1985) and sometimes do not enter these areas even when the food supply increases (Brown and Mate 1983).

Harbour seals appear to move into Comox Harbour and Cowichan Bay and sea lions into Cowichan Bay mainly to feed upon prespawning salmon. Using scat analysis, Olesiuk *et al.* (1990b) reported a sharp increase in the proportion of salmon in the diet of harbour seals in these areas during the fall. Also, seasonal movement into estuaries is widespread in Georgia Strait. Of the estimated 15,800 seals present in Georgia Strait during 1988, about 5% inhabited estuaries during the nonspawning salmon season and 17% during the spawning season (Olesiuk *et al.* 1990a; Olesiuk *et al.* 1990b). Our observations of seasonal abundance of seals and salmon confirm that a strong relationship exists between the peak abundance of seals and the peak biomass of migrating salmon through Comox Harbour and Cowichan Bay.

The seasonal movements of salmon into estuaries does not appear to influence the seasonal distribution of California sea lions and Steller sea lions in Georgia Strait to the extent that it does harbour seals. Although these sea lions are widely distributed in Georgia Strait, Cowichan Bay is the first estuary at which sea lions are known to prey upon salmon. We are

uncertain of the year that sea lions began feeding on salmon in Cowichan Bay. Our first record of sea lions at this locality was Decmber 1984, although sea lions could have begun feeding on salmon there a few years earlier as we did not closely monitor this locality in previous years.

The arrival time of Steller sea lions and California sea lions at Cowichan Bay was likely set by the seasonal migration of these species into Georgia Strait. They arrive mainly in October from summer rookeries and haulouts outside of Georgia Strait (Bigg 1985). California sea lions arrive from sites between Oregon and Mexico and Steller sea lions from sites as far south as California and perhaps as far north as Alaska. The departure of sea lions from Cowichan Bay is much earlier than for the departure from Georgia Strait, which is mainly during May. Both this fact and the results of our current studies on foraging suggest that the departure of sea lions from Cowichan Bay results from a decreasing supply of salmon, rather than the onset of a long distance migration.

2. Group foraging

Harbour seals are usually described as solitary foragers (Scheffer and Sperry 1931; Rae 1973; Renouf *et al.* 1981), although few studies have examined the foraging behaviour of this species. While solitary feeding may be the most common feeding pattern in this species, our studies suggest that group foraging can take place. We have observed group foraging on prespawning salmon in Comox Harbour and Cowichan Bay. Group foraging might be the most effective feeding technique whenever concentrations of large prey are encountered.

The feeding efficiency of individuals presumably increases when foraging on such large prey as prespawning salmon in shallow estuaries and rivers. Optimal foraging theory (Pulliam and Caraco 1984) predicts that in most cases individuals which forage in groups should be more successful at obtaining food than when foraging alone and that the optimal size of the foraging group would be determined by an energy trade off between prey size and time required to find the prey. We did not collect information on the individual foraging success rates of harbour seals when hunting each species of salmon and thus cannot say anything about foraging success in groups of different sizes. However, some support for the prediction that larger groups take larger prey comes from the fact that the size of harbour seal groups increased with an increase in the size of the salmon species eaten. Thus, perhaps the larger prey were more often successfully captured by large groups than by small groups. However, our study cannot rule out an alternate explanation that group size increased because large salmon also took longer for harbour seals to eat. The longer the time to eat the salmon the greater the possibility that opportunistic feeders had to join a group and thus increase group size. The success rate of foraging by individuals in groups of different sizes and on different sizes of salmon will need to be examined in a field study which specifically addresses these issues.

Another aspect of group foraging which needs addressing in a field study is the duration of individual bonds within groups. We were unable to determine whether individuals foraged together only for one feeding bout or

more than one. Tagging studies would provide information on the duration of bonds and the extent of cooperation.

Gearin *et al.* (1988) reported that individual California sea lions which foraged on prespawning steelhead trout at the Hiram M. Chittenden Locks, Seattle, had feeding territories. Thus, this pinniped did not feed in groups like harbour seals. Although we did not investigate the possibility of feeding territories for sea lions at Cowichan Bay, our observations that sea lions fed predominantly alone is in keeping with the findings of Gearin *et al.* (1988).

3. Competition between harbour seals and sea lions

Although harbour seals and sea lions sometimes forage in the same inshore localities along their ranges, no instances have been reported in the literature of direct feeding competition. Our observations suggest that sea lions appeared to displace some harbour seals from the preferred feeding area in Cowichan Bay. This is the first evidence that competition occasionally exists. It is possible that harbour seals were able to compensate for the disturbance by feeding in the preferred site at night. However, we were unable to confirm this possibility because our observations were restricted to daylight hours.

4. Predation impact

Little research attention has been directed toward determining the impact of pinniped predation on prey stocks by direct field observations. However, we believe that this method has good potential particularly for assessing predation impact on prespawning salmon in estuaries and rivers. The method is relatively straight forward when predation rate per hour can be determined and an estimate of the number of each salmon species escaping to spawn is available from local fisheries managers.

Nonetheless, the method has a number of potential biases which need to be examined in the future in order to confirm reliability. For example, we have assumed that all salmon captured by pinnipeds were brought to the surface and thus could be recorded as being eaten. This assumption seems likely to be true for predation on the large prespawning salmon in the shallow waters of estuaries and rivers. Spalding (1964) felt that harbour seals ate small prey below the surface, but brought large prey to the surface to break it apart. Brown and Mate (1983) assumed that all adult chum salmon were brought to the surface in their study of harbour seal predation in Netarts Bay. Similarly, Gearin *et al.* (1988) assumed all predation by California sea lions on steelhead trout at Seattle, Washington, was witnessed.

However, if some individuals of a particular salmon species were not brought to the surface, the predation impact on that species would be underestimated. Such a bias may exist for small salmon, such as jack chinook and jack coho. We suspect that jack salmon, which are the smallest adult salmon, may be eaten underwater before field observers could arrive at the kill site to collect evidence of consumption.

Another possible bias in an impact assessment based on field observations is that the predation rate varies through the day. Being opportunistic feeders, harbour seals and sea lions likely feed upon salmon whenever this prey is most easily available and, because prespawning salmon are in the estuaries and rivers all day that they are available for predation all day. We assumed that the rate was the same throughout the daylight hours and about half this rate at night. However, this may not be true. The rate could vary by time of day or by tide height. It is possible that these pinnipeds have preferences to feed at certain times or tides or that the behaviour of salmon to the seal is influenced by these factors. Also, the availabiiity of each salmon species to these pinnipeds might differ relative to one another.

Our field observations suggests that harbour seals have a relatively low level, <10%, of predation on prespawning pink, coho and chum salmon in Comox Harbour and Cowichan Bay. A similar level of 1-7% was reported by Brown and Mate (1983) for harbour seals at Netarts Bay. However, a high predation rate (46%) exists on the fall run of chinook in Comox Harbour. This particularly high rate appears to result from two reasons. First, the fall chinook run is small and is preyed upon by a large population of seals. The number of chinook in the Comox River is far smaller than for pink, coho and chum salmon. Gearin *et al.* (1988) similarly reported a high predation rate (43%) during 1986-87 by California sea lions on a small population of steelhead trout at Seattle. Noteworthy is the fact that the impact of harbour seal predation was probably much less in the recent past because the current chinook stock of 1300 individuals has been depleted by overfishing and habitat loss during the past two decades. During the 1950's chinook spawning escapement in Comox Harbour was much higher, averaging 6000 fish (Hancock and Marshall 1985).

The second reason for the high predation rate on the fall run of chinook is that these chinook are vulnerable to predation not just in the estuary of Comox Harbour, but also in the lower reaches of the slow moving Puntledge River where almost half of the predation took place. Many other river systems in Georgia Strait are not as slow moving as the Puntledge River and would likely provide less suitable foraging areas for seals. It should be noted here that, because of the small population of chinook, any biases in the estimate of the number of chinook spawning or in the number eaten will disproportionately alter the predation rate compared to the same biases for pink, coho and chinook.

Direct field observations and scat analysis are both useful methods to determine predation impact. Each method has assumptions which are sometimes difficult to verify. However, each provides a different perspective in predation impact assessment; scat analysis is useful for larger scale, general studies aimed at establishing the relative importance of different prey, while observational studies are restricted in area and time to determine the impact on a specific prey species. Thus, where feasible both observtional and scat analysis methods should be used.

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Table 2. Number of hours of observation and number of salmon kills recorded (in parentheses) at Comox Harbour and Cowichan Bay for harbour seals and sea lions during August-December 1989

Month	Harbour seals			Sea lions	Total
	Comox Harbour		Cowichan Bay	Cowichan Bay[1]	
	Estuary	Puntledge River			
Aug	37 (34)				37 (34)
Sep	15 (18)	14 (16)	2 (4)		31 (38)
Oct	8 (22)	8 (16)	38 (81)	(18)	54 (137)
Nov	4 (9)	9 (8)	24 (30)	(74)	37 (131)
Dec	2	2 (2)	2		6 (2)
Total	66 (83)	33 (52)	66 (115)	(92)	165 (342)

[1]Effort was the same as for harbour seals in Cowichan Bay.

Table 3. Number of salmon kills, by species, for each foraging group size of harbour seals and sea lions at Comox Harbour and Cowichan Bay.

A. Harbour seals at Comox Harbour

Species eaten	Sample size	# of individuals in group 1	2	3	4	5	6	7	8	9	Mean
Chinook	37	6	5	10	7	4	4			1	3.4
Coho	20	2	7	4	5	1	1				3.0
Pink	22	14	6	2							1.5
Chum	35	1	13	10	8	2	1				3.0
Unknown	21	2	9	6	2	1	1				2.7
Total	135	25	40	32	22	8	7			1	2.8

B. Harbour seals and sea lions (in parentheses) at Cowichan Bay.

Species eaten	Sample size	Group size 1	2	3	4	5	6	Mean
Chinook	6	2	2	1	1			2.2
Coho	4 (9)	1 (9)		1	1		1	3.5 (1.0)
Chum	11 (22)	2 (19)	5 (3)	4				2.2 (1.1)
Unknown	2 (17)	2 (16)						1.0 (1.1)
Total	23 (48)	7 (44)	7 (3)	6 (1)	2		1	2.3 (1.1)

Table 4. The number at spawning of each salmon species, estimated number eaten by harbour seals and sea lions during a range between daylight hours (left)and 24 hours and the mean percent eaten of each salmon species entering Comox Harbour and Cowichan Bay during 1989. Also given is a comparison between the mean biomass of each salmon species eaten by harbour seals in Comox Harbour and Cowichan Bay during 1989 based on the current study and during 1988 based on scat analysis given by Olesiuk et al (1990, Table 7).

Species	Number spawning[1] 1989 C	Number eaten 1989 Range B	Number eaten 1989 Mean %[2] A	Biomass eaten mt 1989[3] Range	Biomass eaten mt 1989[3] Mean	Biomass eaten mt 1988
A. Harbour seals, Comox Harbour						
Pink	20,000	706-1135	4.4	1.2- 1.9	1.6	2.3
Coho - nonjack	15,000	974-1816	8.5	2.5- 4.7	3.6	3.7
- jack[4]	12,000	-	-	-	-	-
Chum	38,000	1987-4116	7.4	9.3-19.3	14.3	22.2
Chinook						
Fall - nonjack	1,300	797-1417	46.0	5.3- 9.5	7.4	0.5
- jack	100	-	-	-	-	-
Summer - nonjack	900	-	-	-	-	-
- jack	50	-	-	-	-	-
Steelhead[5]	300	-	-	-	-	-
Total	87,650	4022-7689		18.4-35.5	26.9	28.7
B. Harbour seals, Cowichan Bay						
Coho - nonjack	17,000	151- 303	1.3	0.4- 0.8	0.6	1.0
- jack	400	-	-	-	-	-
Chum	45,000	440- 881	1.4	2.1- 4.1	3.1	7.4
Chinook						
Fall - nonjack	5,000	-	-	-	-	0.5
- jack	7,500	-	-	-	-	-
Summer - nonjack	100	-	-	-	-	-
- jack	0	-	-	-	-	-
Total	75,000					8.9
C. Sea lions, Cowichan Bay						
Coho - nonjack	17,000	331- 662	2.8	0.9- 1.7	1.3	-
- jack	400	-	-	-	-	-
Chum	45,000	844-1688	2.7	4.0- 7.9	6.0	-

Table 4 (cont'd) Footnotes:

[1]Data from C. Beggs (pers. comm. April 1990, Dept. Fisheries and Oceans, Comox, British Columbia) and R. Tupniak (pers. comm. April 1990, Dept. Fisheries and Oceans, Duncan, British Columbia).

[2]$A = \frac{100(\text{mean of B})}{(C + \text{mean of B})}$

[3]Product of the number of each species eaten and the average mass (kg) of individuals of each species. Average mass for pink = 1.7, nonjack coho = 2.6, chum = 4.7, summer nonjack chinook = 4.3, fall nonjack chinook = 6.7; jack coho = 0.5, summer jack chinook = 0.9, fall jack chinook = 1.4,; source C. Beggs (pers. comm. April 1990, Dept. Fisheries and Oceans, Comox, British Columbia).

[4]Jacks are small precocious males. The mean masses (kg) of individuals are: jack coho = 0.5, summer jack chinook = 0.9, fall jack chinook = 1.4,; source C. Beggs (pers. comm. April 1990, Dept. Fisheries and Oceans, Comox, British Columbia).

[5]Mean individual mass = 3.6 kg

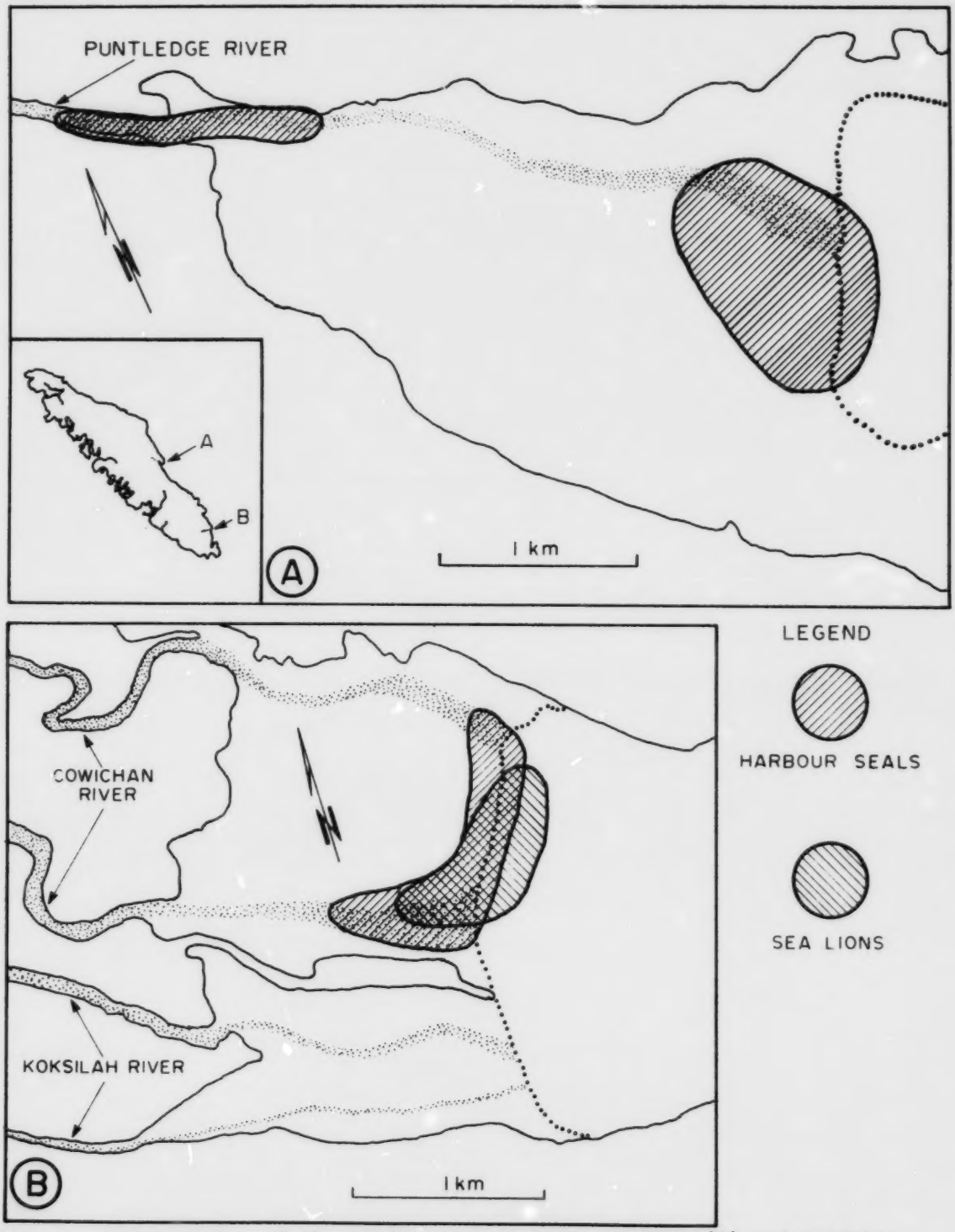

Fig. 1. Illustration of the study areas at Comox Harbour (A) and Cowichan Bay (B) showing the rivers which flow into them, the approximate drainage pathways over the estuaries, the 10 m depth contour (dotted line) and the main salmon feeding areas used by harbour seals, Steller sea lions and California sea lions during 1989.

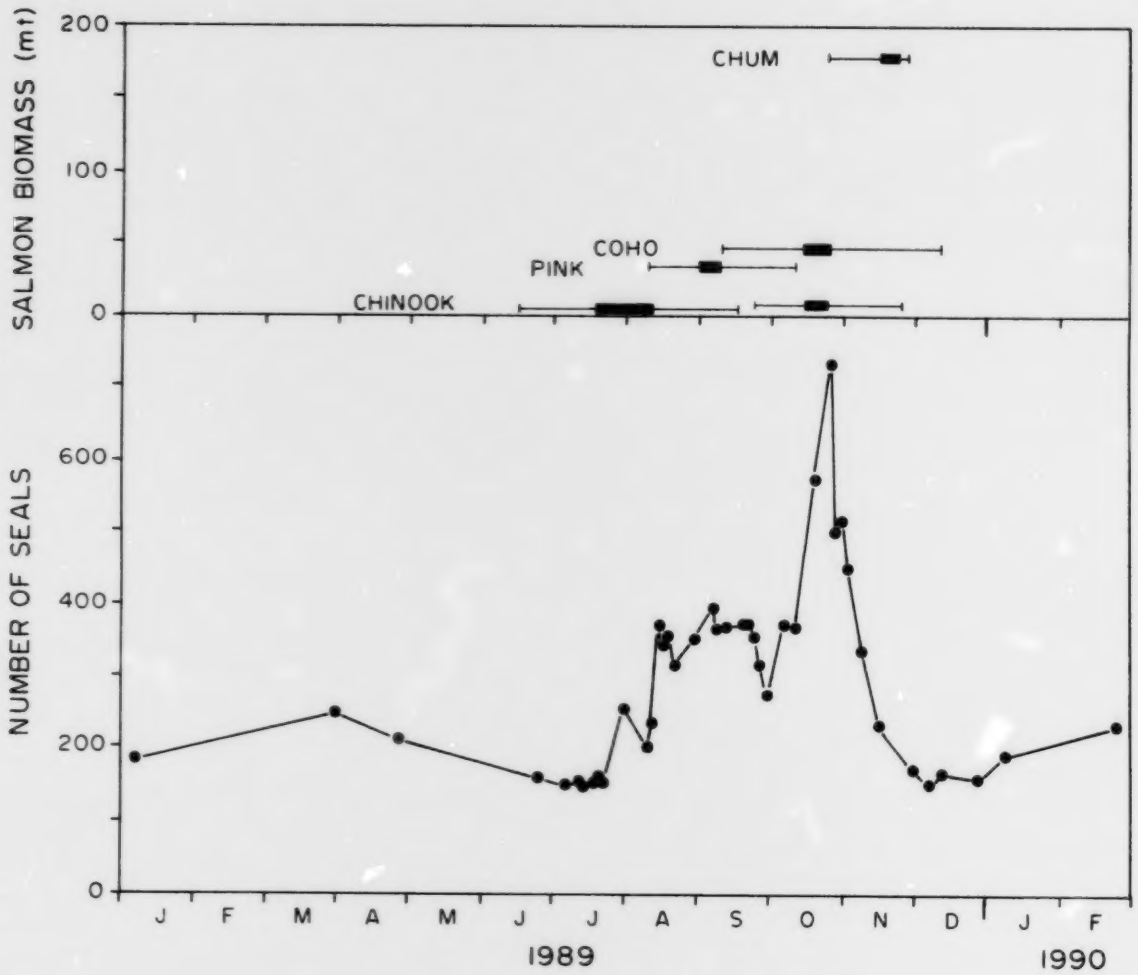

Fig. 2. Seasonal change in the number of harbour seals counted in Comox Harbour (estuary and Puntledge River) during 1989-90, the typical upper river ranges of spawning season (thin horizontal lines) and main spawning season times (thick horizontal lines) for summer and fall runs of chinook salmon and for pink, coho and chum salmon and the biomass of each salmon species spawning in 1989. Data on spawning season and biomass provided by C. Beggs (pers. comm. April 1990, Dept. Fisheries and Oceans, Comox, British Columbia). The seasonal timing of salmon in Comox Harbour is likely to be 1-2 weeks earlier than the spawning season indicated for the upper reaches of the river.

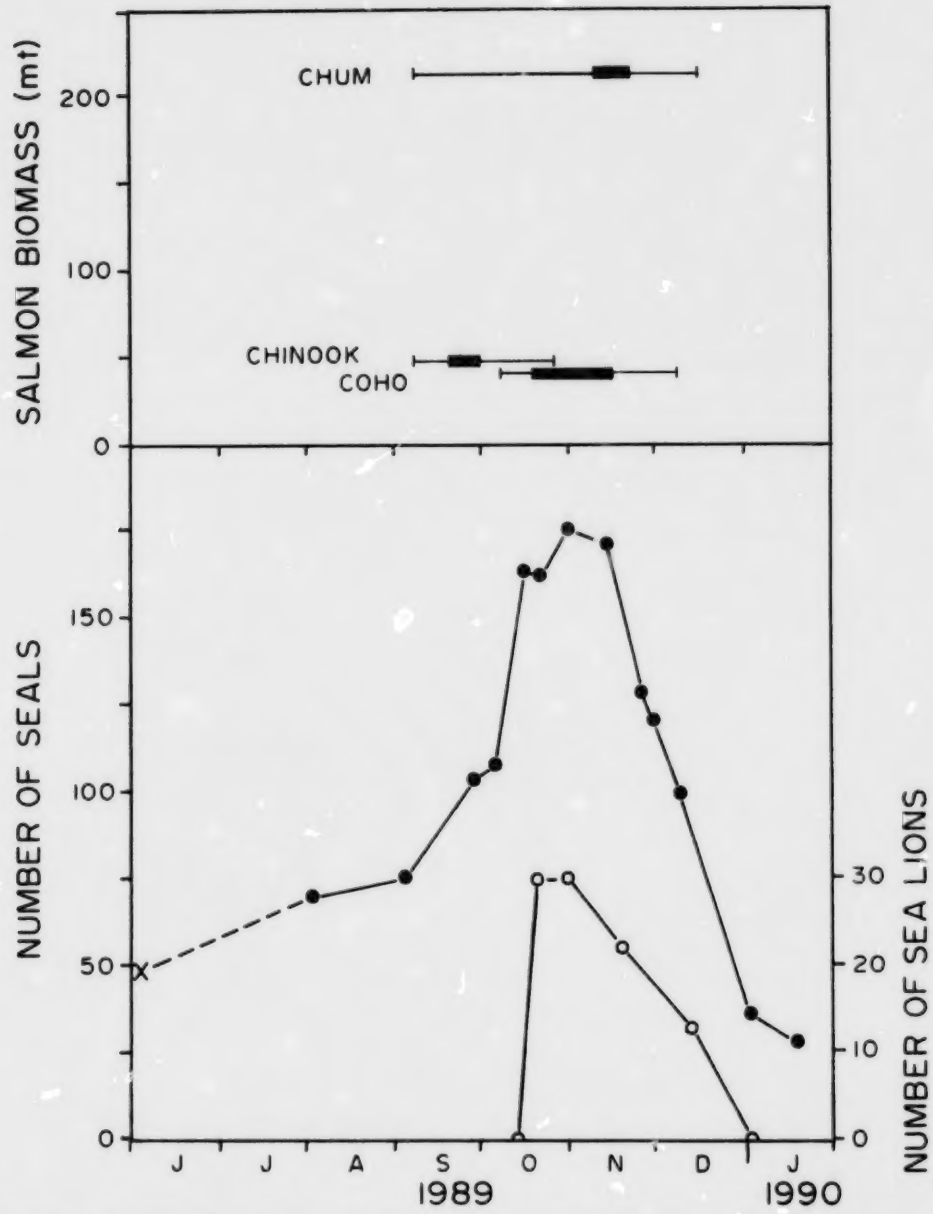

Fig. 3. Seasonal change in the number of harbour seals (solid circles; X=1988) and sea lions counted (open circles) in Cowichan River during 1989-90, the typical spawning season ranges (thin horizontal lines) and main spawning season times (thick horizontal lines) for the fall run of chinook salmon and for coho and chum salmon and the biomass of each salmon species spawning in 1989. Data on spawning season and biomass provided by R. Tupniak (pers. comm. April 1990, Dept. Fisheries and Oceans, Duncan, British Columbia). The seasonal timing of salmon in Cowichan Bay is likely to be 1-2 weeks earlier than the spawning season indicated in the upper reaches of the rivers.

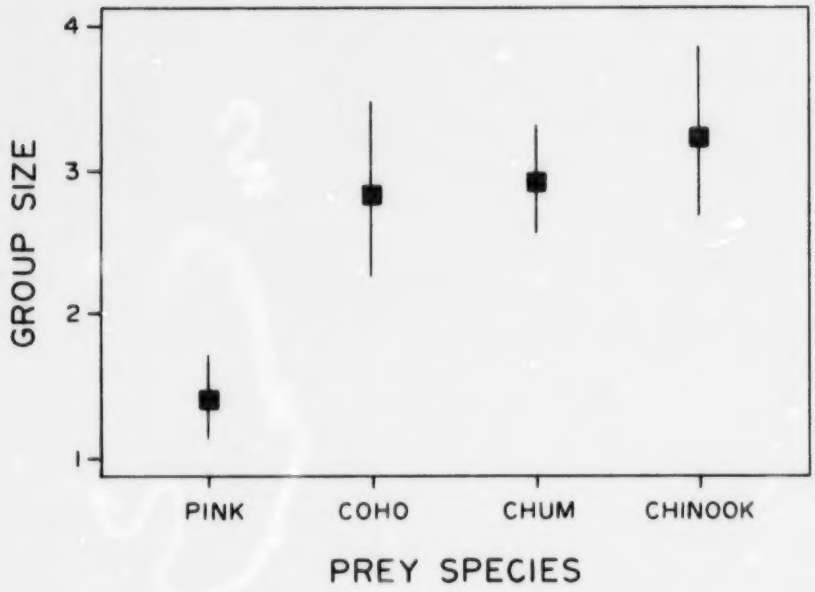

Fig. 4. Mean group size and 95% confidence limits of harbour seals foraging on pink, coho, chum and chinook salmon at Comox Harbour (estuary and Puntledge River) during 1989.

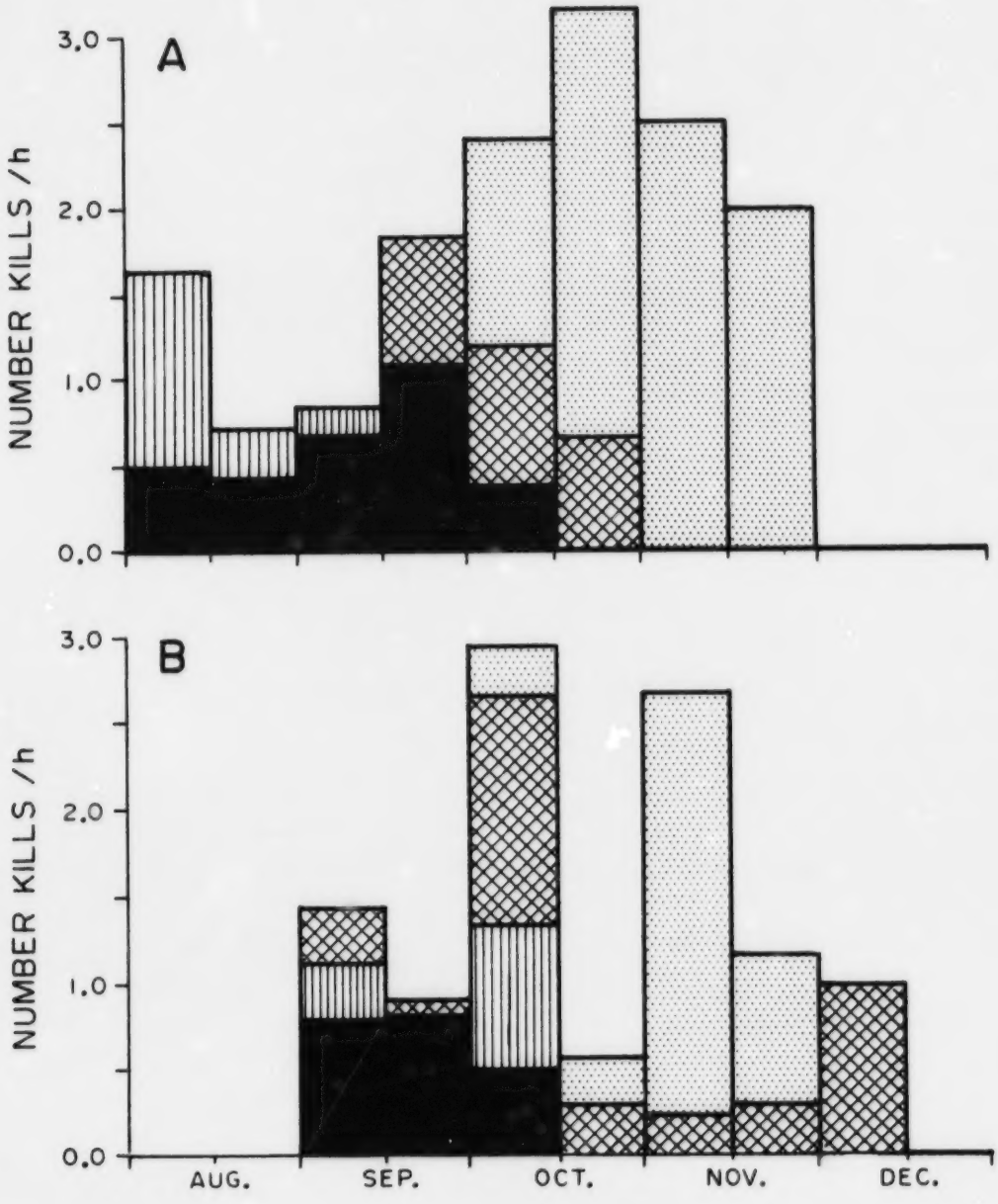

Fig. 5. Number of nonjack salmon eaten per hour by harbour seals in the Comox Harbour estuary (A) and in the Puntledge River (B) by 0.5 month intervals during 1989. Salmon species key: solid is chinook, vertical stripes is pink, cross hatching is coho and stippling is chum salmon.

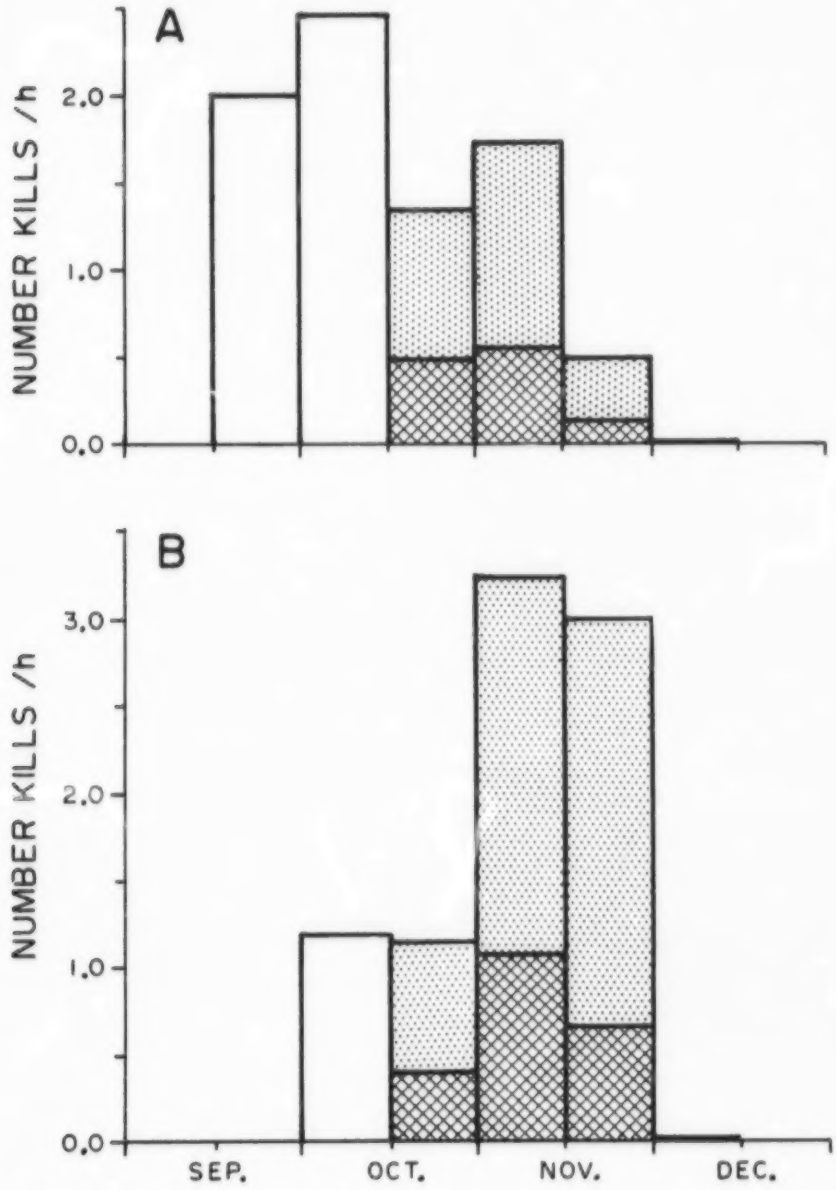

Fig. 6. Number of nonjack salmon eaten per hour by harbour seals (A) and sea lions (B) in Cowichan Bay by half month intervals during 1989. Salmon species key: open is unknown species, cross hatching is coho and stippling is chum salmon.